

# REVIEW OF THE DISTRIBUTION OF THE COMMONER ANIMALS IN LOWER SILURIAN MARINE BENTHIC COMMUNITIES

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ABSTRACT. The distribution of the commoner species, most of which are brachiopods, in thirty large collections from the late Llandovery of the Welsh Borderland gives extra data on the previously published *Lingula*, *Eocoelia*, *Pentamerus*, *Stricklandia*, and *Clorinda* communities. The constituents of the communities were not usually interdependent, but lived together in comparable habitats with similar external parameters. The depths at which the communities lived are reviewed and it is concluded that the total depth range of the community spectrum was probably less than 200 m.

STUDIES of brachiopod-dominated associations of lower Silurian age from the Welsh Borderland began over twenty years ago, and these associations were subsequently grouped into animal communities (Ziegler 1965; Cocks 1967; Ziegler *et al.* 1968*a*) which were distributed stratigraphically into organized patterns subparallel to the inferred shoreline (Ziegler *et al.* 1968*b*). It is now opportune to review some aspects of these studies, which came before most scientific work on Palaeozoic communities of other ages; to present more data on the variation within the described communities; and to discuss some aspects of the ecology of the individual constituents.

Exceptional preservation, such as that in the Cambrian Burgess Shale or the Carboniferous Mazon Creek beds, sometimes enables a palaeontologist to glimpse the whole range of flora and fauna to be found on the sea floor, and to compare it with that living today. However, it has long been realized that the average preserved fossil collection from the vast majority of ordinary localities represents only a small proportion of the original biota, both in biomass and diversity, even assuming that the fossils have not been carried dead into the area of deposition. Thus some palaeontologists have questioned the use of the word 'community' when describing repetitive associations of fossils such as those from the Welsh Borderland Llandovery rocks. However, we are unrepentant since, as can be seen by comparison with modern-day situations, such associations assuredly reflect the original communities of which they formed part, and we feel that the shorthand terminology of referring to these preserved associations as 'communities' is justified. We continue to define our communities in a relatively broad way (Cocks and McKerrow *in* McKerrow 1978), unlike the narrower community groupings of Boucot (1975).

## *Upper Llandovery communities*

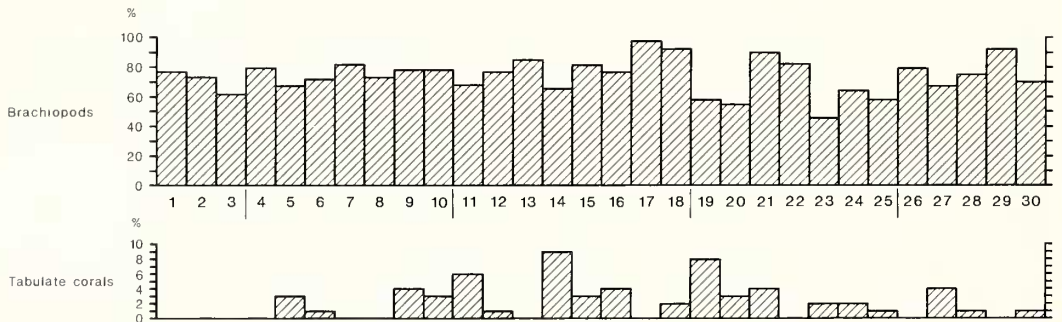
The Llandovery is an exceptionally good period to study clastic level-bottom animal communities for several reasons: first, there is an excellent framework for accurate correlation (Cocks 1971) using both graptolites and shelly fossils, in particular by using the evolution of selected brachiopods such as *Stricklandia* (Williams 1951 and later authors) and *Eocoelia* (Ziegler 1966); secondly, because there was a very widespread distribution of a single faunal province due to the relative nearness of several land masses at that time (Cocks and Fortey 1982, fig. 5): the same communities are very widely distributed across North America, Europe, and parts of Asia; and thirdly, because of the substantial erosion during the glacioeustatic regression at the Ordovician-Silurian boundary, the edges of the Llandovery shelves were relatively well marked (like the continental shelves of the present day following the Pleistocene glaciation), and can be recognized using sedimentological criteria as well as by the distribution of benthic communities.

All the communities discussed in this paper lived in the open shelf sea and on clastic bottoms. We assume that the salinity of all the environments was normal marine, with the exception of some of the near-shore *Lingula* community. Whether or not all of the constituents of the *Lingula* community, such as the large bivalves, some tentaculitids and brachiopods such as *Stegerhynchus decemplicatus*, were able to thrive in reduced salinities is more doubtful. There are no carbonate deposits included in the samples described, although the same named communities are known from carbonate sediments, for example in North America and Estonia; but other associations are also found in those places, including some associated with bioherms and shallow-water micrites, which are outside the scope of this review.

We have reidentified the specimens in 30 of the 94 collections originally made by Ziegler and Cocks (Ziegler *et al.* 1968*b*, Appendix 1) from the late Llandovery of the Welsh Borderland. The real numbers in each collection are greater than the totals shown in text-figs. 1 and 2 because only the most commonly occurring brachiopod or molluscan valve was counted; for example, in Collection 13 there were 104 pedicle valves and 85 brachial valves present of *Pentamerus oblongus*, but only the 104 were included in the collection total shown of 220. Thus the 30 collections represent well over 10,000 specimens.

The percentages present of all of the different species in the thirty collections were calculated, and the total numbers of species are shown in text-fig. 1*a* broken down into brachiopods and other phyla. The average number of brachiopod species in each community increases from 4 in the *Lingula* community to 20 in the *Clorinda* community, but by contrast the average number of species other than brachiopods does not vary so much, although there is a general progressive increase in total diversity from the *Lingula* to the *Clorinda* communities. The total proportions of brachiopods are also tabulated (text-fig. 1*b*) and, although the brachiopods vary from 46% to 97% of the total in any one collection (average 72%), there is no general pattern of relative brachiopod dominance in any one community, and the average remains surprisingly constant between the communities.

Collection number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Locality (Ziegler <i>et al.</i> 1968, p.780-1)	24	32	34	35	44	11	4	46	43	1	37	63	59	45	52	53	13	16	12	73	40	68	70	69	54	60	49	58	55	56
Total fossils	373	52	185	119	348	267	324	662	204	273	351	1044	220	300	122	122	126	141	91	522	185	293	330	409	211	163	333	167	360	381
No. of species	brachiopods			EOCOELIA							PENTAMERUS					STRICKLANDIA					CLORINDA									
	non-brachiopods			av. brachs. 9							av. brachs. 10					av brachs 10					av. brachs 20									
	Total			av. non-br. 13							av non-br 9					av. non-br. 13					av. non-br 12									
	16	10	11	15	20	20	26	30	21	22	28	30	15	25	12	13	15	16	13	27	21	15	37	24	20	25	40	27	29	36
Community	LINGULA			EOCOELIA							PENTAMERUS					STRICKLANDIA					CLORINDA									
	av. brachs 4			av. brachs. 9							av. brachs. 10					av brachs 10					av. brachs 20									
	av. non-br. 9			av. non-br. 13							av non-br 9					av. non-br. 13					av. non-br 12									
	13			22							19					23					32									



TEXT-FIG. 1. Numbers of brachiopod and other species in thirty collections from the late Llandovery of the Welsh Borderland, and the average numbers of species in the various animal communities described by Ziegler *et al.* (1968*a*). Middle row, proportions of brachiopods (shaded) to species of other phyla in the same collections. Bottom row, percentages of tabulate corals in the same collections.

To construct text-fig. 2, only genera that occur as 10% or more in more than one collection were selected for inclusion. The total distributions of these genera in all thirty collections are shown, so that the relative abundance and community ranges may be seen at a glance. Superimposed on the community structure are some distributions caused by local clumping. To eliminate these random effects we do not show forms that occur as over 10% in only one collection, and these are the brachiopods *Dolerorthis* (10% in Collection 11), *Isorthis* (11% in Collection 9), *Salopina* (10% in Collection 9), *Brachyprion arenacea* (16% in Collection 12), and '*Meristina*' *furcata* (12% in Collection 13), and the bryozoan *Hallopora* (16% in Collection 16).

From text-fig. 2 it can be seen that the community range of each taxon varied widely both in selectivity and abundance, from *Pentamerus*, which is rare outside its named community but very abundant within it, through *Atrypa*, which occurs in the *Eocoelia* to *Clorinda* communities but with a weak indication of an abundance maximum in the *Pentamerus* and *Stricklandia* communities, to streptelasmatic corals, which (apart from their absence in the *Lingula* and part of the *Eocoelia* communities) are widespread throughout the rest of the community spectrum with little indication of an abundance maximum. Although the brachiopod diversity increased steadily up to the *Clorinda* community, the largest brachiopods are to be found in the *Pentamerus* and *Stricklandia* communities; not just the eponymous pentamerides but the bigger strophomenides such as *Leptostrophia* and the larger species of *Leptaena* and also the larger specimens of atrypids. We have no quantitative data on the biomass involved, but from our collecting we would estimate that these mid-shelf communities appear to have been the areas representing the optimal conditions for the growth of large brachiopods, in contrast to the higher-energy shallower environments on the one hand and the relatively plankton-starved deeper water on the other. Further aspects of the size and feeding efficiency of some Silurian brachiopods were considered by Fürsich and Hurst (1974).

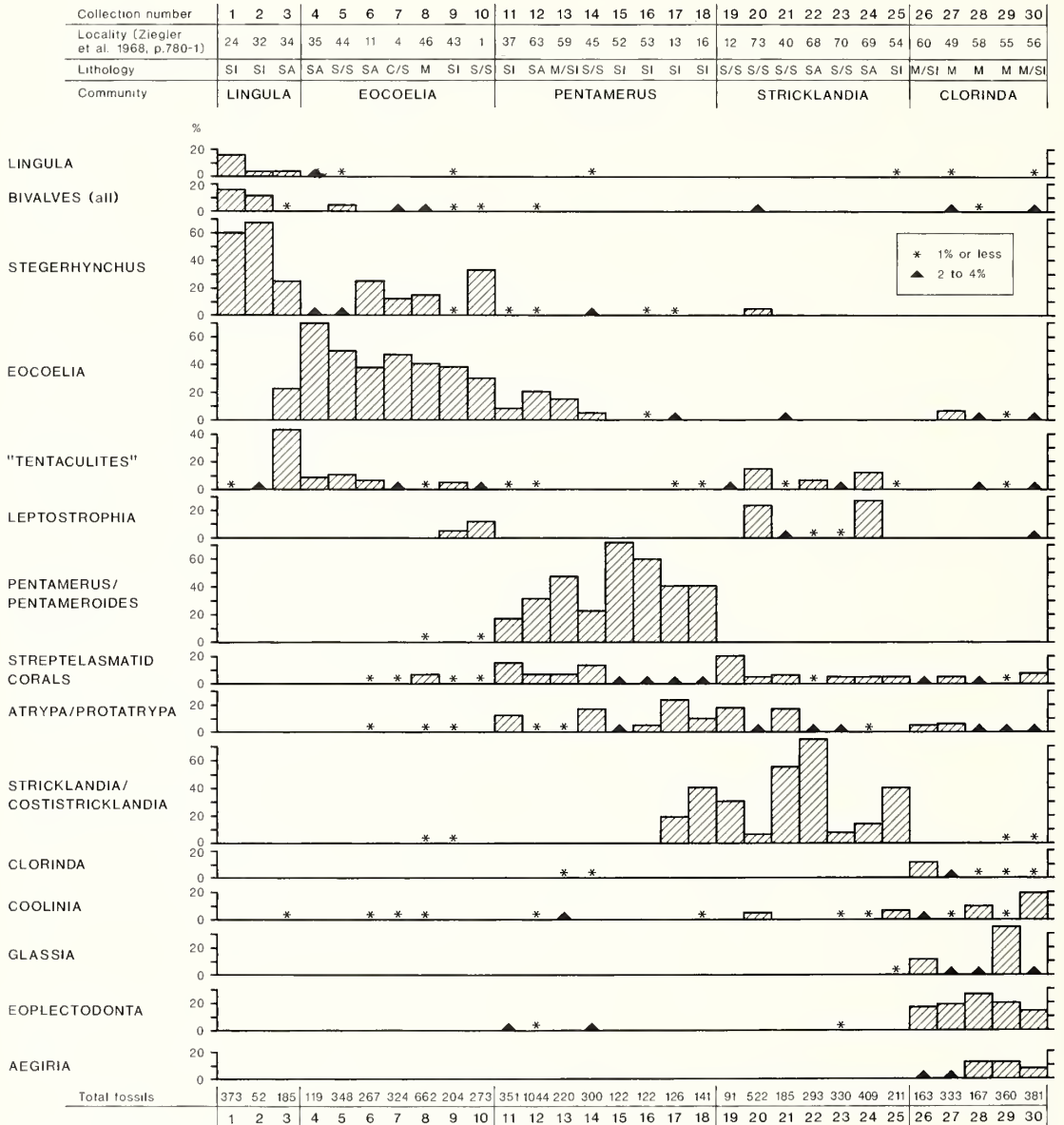
The Llandovery communities are made up of an agglomeration of animals, each of which had a distinct but specific tolerance to a range of marine bottom conditions, but which do not appear to have had any marked degree of mutual interdependence. Of course there are exceptions, for example, some of the bryozoans and cornulitids needed larger shells for their attachment, but most of the individual brachiopods, trilobites, molluscs, corals, and other larger benthos would have been unaware of, and independent from, their neighbours. The normal relationships between interdependent members of the same community today are either as successive members of a food chain or as providing shelter or anchorage. In the Llandovery most food chains were not long; the vast majority of the fauna were suspension feeders or deposit feeders. The numbers of predators and scavengers was probably small, and confined to echinoderms, cephalopods, a small minority of arthropods such as eurypterids (not phyllocarids, *contra* Watkins 1979, p. 249), and, perhaps, some soft-bodied worms. The gastropods present were all archaeogastropods which were almost certainly algal grazers or to a lesser extent deposit feeders; there are no confirmed predatory gastropods of Silurian age. Thus the distribution of the sedentary benthos must have been controlled partly by the availability of food and partly by physical factors (Fürsich and Hurst 1974). When two or more species persistently occur together, particularly in substantial numbers, then this indicates that the external parameters would have been suitable for them all, but this does not mean that they need have been biologically interdependent.

#### *Relationships with depth and sediment type*

Since the work of Ziegler (1965) there has been dispute as to the extent to which the distribution of Llandovery communities is (a) depth related and (b) dependent on sediment type. Let us examine these in turn. Critics such as Watkins (1979, p. 250) have pointed to the discrepancy between the interpretation of Ziegler *et al.* (1968b, fig. 13), which shows a smooth gradient across the late Llandovery shelf and communities, and the subsequent sedimentological work of Bridges (1975, fig. 11A), which shows a more varied gradient, and in particular an emergent Longmynd spur in Shropshire at that time. In fact a situation such as the latter was explicitly envisaged by Ziegler *et al.* (1968b, caption to fig. 12). Their fig. 13 was inevitably generalized, but an analysis of the sediments

and faunas round the Longmynd shows that they do yield progressively more off-shore ecogroups in each section as the transgression proceeded.

The best proof that the Llandovery communities were depth-related comes from the studies of eustatic changes in Silurian sea levels (McKerrow 1979; Johnson 1980; Johnson *et al.* 1981; Colville and Johnson 1982). The mere fact that these studies show that the communities shifted seawards or shorewards synchronously on the various different palaeocontinents indicates conclusively that the water depth and the communities are directly linked, and that the sequence of ecogroups is



TEXT-FIG. 2. Commoner taxa in thirty collections from the late Llandovery of the Welsh Borderland (only taxa occurring as more than 10% in two or more collections are included). The collections are attributed to the various animal communities described in Ziegler *et al.* (1968a).

everywhere the same during late Llandovery time. Of course depth is not directly linked to distance from shore—the width of the community bands seen in the central and eastern United States can be over 200 km per community, a tenfold increase over many of the band widths seen in the Welsh Borderland.

The actual depths involved have been debated. Ziegler (1965) calculated from the displacement of communities by lava flows in Pembrokeshire and Gloucestershire that the depth ranges were in 'tens of feet rather than hundreds of feet', but more rigorous field work in the same areas left these conclusions doubtful. Hancock *et al.* (1974) postulated depths of up to 1500 m for later Silurian communities, although this view was subsequently modified by Hurst (1976) after Shabica and Boucot (1976) had pointed out that the cephalopods were not imploded in the deepest assemblages, indicating that the maximum depth range was probably less than 600 m.

We incline to a shallower figure. The distinctive porous coenosteoid structure of heliolitid corals is also found in Recent scleractinian corals (B. R. Rosen pers. comm.), but amongst which it is confined almost exclusively to zooxanthellates, i.e. those corals that are symbiotic with dinoflagellate algae (Rosen 1981). Zooxanthellate corals do not live in depths greater than 240 m and the vast majority of genera live in water shallower than 100 m (Rosen 1977). In the Silurian, heliolitids are most common in carbonate bioherm environments, but they are a subsidiary element of the tabulate coral fauna (text-fig. 1c) in clastic environments, being recorded from the *Eocoelia*, *Pentamerus*, and *Stricklandia* communities up to Collection 23 of text-fig. 1, 2. This suggests that the *Stricklandia* Community inhabited depths of less than about 200 m, and probably even less than 100 m, leaving only the *Clorinda* Community as a candidate for deeper water in Llandovery times. Offshore of the *Clorinda* community the diversity and abundance of shelly benthos drops rapidly (the Marginal *Clorinda* Community of Cocks and Rickards 1969). Although it is dangerous to compare the relative widths of community band distribution, such a comparison in the Welsh Borderland indicates that the *Clorinda* community is unlikely to have occupied substantially more space and width on the sea-floor than the *Stricklandia* community, and thus a total depth range of not more than 250 m and perhaps less than 150 m seems the most likely. If it was greater then the community shifts caused by eustatic changes in sea-level would indicate that the real figures for the rising or lowering of the water would have been improbably high; for example, if the *Clorinda* community had really occupied a depth band of from 200 m to 600 m, then a 400 m rise in sea-level (which could have been caused by a combination of eustasy and local tectonics) would have been needed to change from the *Stricklandia* to the Marginal *Clorinda* communities, a shift seen in many other places as well as the Welsh Borderland. It would seem that this is less probable than the more modest changes needed if it were postulated that the total *Lingula* to *Clorinda* community depth range was less than 200 m.

Brenchley and Cocks (1982, p. 807) also concluded that the depth spectrum of the latest Ordovician communities found in the Oslo region, Norway, was unlikely to have been much more than 100 m; this figure was based both on an analysis of the sedimentological structures present and also on estimates of the depth differences likely to have been involved in the contemporary glacio-eustatic fall in sea-level.

In normal non-glacial littoral and sublittoral environments today the clastic sediments found can be of any grain size from cobbles to mud, but towards the deeper parts of the shelf (in areas not subject to major tectonic activity) the coarser fractions are progressively eliminated such that only silt and mud are common at the outer shelf margin. On text-fig. 2 we have indicated the sediment type for each of the Llandovery collections and these range from conglomeratic sandstone (C/S) through sandstone (SA), silty sandstone (S/S), siltstone (SI), muddy siltstone (M/SI) to mudstone (M). It can be seen that, although there is a higher proportion of mudstones in the *Clorinda* community collections, nevertheless there is a very poor correlation between sediment type and individual communities, an obvious example being the *Eocoelia* community which has been found in the widest variety of sediments from conglomeratic sandstones to mudstones. The same applies to individual species and genera, e.g. *Stegerhynchus* (text-fig. 2). Of course this does not mean that all benthic animal communities are or were substrate independent, but merely that the dominant shelly benthos of Llandovery age, such as brachiopods, corals, and tentaculitids, were mostly epifaunal, and,

assuming that a suitable spat attachment surface had been found, the individuals were tolerant of a wide range of substrates. Infaunal forms and burrowers would have been more likely to have been sediment specific, but these were not common in Llandovery time, and even lingulids have been found in a wide range of sediment types and grain size. Trilobites, on the other hand, appear to have been more directly linked to particular substrates in some cases, but no trilobite is recorded at more than 5% in the thirty collections (*Warburgella* in Collection 30 and *Phacops s.l.* in Collection 23), and only *Encrinurus* and *Dalmanites* are known from many of the shallower-water localities. Some trace fossils are also considered to have been related to bathymetry (Seilacher 1967).

It is difficult to assess the effect of varied turbulence on the animals present. The greater the water turbulence the greater the food supply, but the greater the strength needed for pedicle attachments, holdfasts, etc., which was probably a direct factor in the distribution of some of the more common taxa. Most strophomenides, for example, thrived best in lower energy environments, and the large pentamerides were clearly less vulnerable to wave damage in the middle part of the shelf, particularly since their pedicles were no longer functional as adults. The effects of turbidity are better known. Most brachiopods can clean any excess sediment from their lophophores, unlike most bivalves, whose gills become clogged fairly rapidly (Steele-Petrović 1975). Corals can also survive after fairly turbid episodes, although they will be killed if the sediment covers the polyps completely.

#### *Comparison with communities of other ages*

It is instructive to compare the Silurian palaeoecological regime with those both earlier and later. In the Cambrian, although most communities are dominated by trilobites and are thus related to sediment type, brachiopods appear to have chiefly occupied a single, relatively shallow-water community niche, with the middle to deeper shelf inhabited mostly by other phyla. During the Ordovician there was a gradual spatial expansion of brachiopods, crinoids, and corals. Lockley's review (1983) suggests in the text that Ordovician communities were very sediment specific; however, the actual data that he presents (1983, text-fig. 6) only loosely bears out his assertion in that just 5 out of 24 communities are found in a single sediment type, and the remaining 19 occur in two or more sediment types, and, moreover, Lockley's sediment categories are very broad. It seems more probable that, at least in post-Arenig times, the distributions of Ordovician brachiopods were also depth-related in a general way. Certainly by late Ashgill times, the associations were distributed in a regular order across the shelf, as can be demonstrated in the well-preserved regressive sequence seen around Oslo, Norway (Brenchley and Cocks 1982); and because the shelf sediments there are so similar throughout (mostly varieties of lime-mud), some other factor more directly related to water depth must be invoked to account for the community distribution.

After the Llandovery there were changes in the community structure, partly due to extinctions of some of the dominant forms, which resulted in changes in the relative abundances of certain families and genera; Calef and Hancock (1974), Hurst (1975), and Watkins (1979) have described these later Silurian communities. During the Devonian, bivalve autecology underwent a dramatic change to exploit many more infaunal as well as semi-faunal and epifaunal habitats. From that time onwards molluscan-dominated benthic communities became much more common than hitherto, and the infauna much more dominant than the epifauna. Some Silurian ecogroups, such as the shallow-water lingulid-rhynchonellid associations, persisted into Carboniferous or even later times, but the complete spectrum of brachiopod-dominated communities across the entire shelf is seldom fully developed after Devonian times. However, the autecology of individual brachiopod genera and species continued to evolve so that they could live in every-increasing absolute water depths, culminating in the abyssal forms known living today; although even now most brachiopods live in water shallower than 200 m.

The time from the later Ordovician to the Devonian was that in which the brachiopods were the dominant forms of shelly benthos across the widest variety of habitats, and thus this was the period when brachiopods can be used as indices for the whole spectrum of level bottom clastic communities. It is these communities that were more directly depth related, in contrast to some others in earlier and later times.

*Acknowledgements.* We thank N. J. Morris, B. R. Rosen, and other colleagues for discussion. This paper formed a contribution to the Symposium on Autecology of Silurian Organisms at Glasgow, September 1983 (IGCP Project 53—Ecostratigraphy).

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Manuscript received 13 July 1983

Revised manuscript received 23 January 1984